

Fecundity and survival advantages of an exotic gastropod compared to a native species

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Abstract: In Argentina the exotic snail *Physa acuta* Draparnaud, 1805 is predominant in environments previously inhabited by the native species *Stenophysa marmorata* Guilding, 1828, raising the question of whether this could have occurred because of differences in survival or reproductive strategies. To analyze the life cycle of these two species, I used the horizontal-life-table method and considered the number and proportion of viable of eggs per oviposition. Although both species suffered a high degree of mortality during the first weeks after oviposition, both the rate and the force of mortality was much greater during the reproductive period, so that the survival curve was not as markedly concave as with other gastropods. *Physa acuta* survived longer than *S. marmorata*, began its reproductive period earlier, and had a longer and more continuous reproductive stage. The number of ovipositions per snail was not different between the two species; but since the mean number of eggs per oviposition was higher in *P. acuta*, fecundity was likewise higher. The increase in fecundity was accompanied by an enhancement of the mortality rate in *S. marmorata*. The percentage of viable eggs was higher in *P. acuta* than in *S. marmorata*, but fecundity increased with age in both species. Life expectancy, reproductive value, and net reproductive rate were higher in *P. acuta*. The success of the exotic species *P. acuta* in the native habitat of *S. marmorata* could be explained in part by the former's earlier sexual maturation, higher reproductive potential, and greater longevity. Further field and laboratory studies are needed to demonstrate the existence of interspecific competition between these two gastropods.

Key words: life cycle, Physidae, reproduction, survivorship, introduced species

The invasion of aquatic environments by freshwater molluscs may have a negative impact on local biodiversity (Mack *et al.* 2000, Rahel 2002) and public health because many species, especially gastropods, may be intermediate hosts for waterborne parasites (Malek 1980). The pulmonate snail *Physa acuta* Draparnaud, 1805 is an invasive species, able to disperse rapidly, colonize new areas, particularly within disturbed environments, and attain high densities (Winterbourn 1980, Brackenbury and Appleton 1993). This species has become established in many parts of the world and has impacted native snails. In South Africa, for example, *P. acuta* proved better able to exploit newly disturbed environments than the native *Bulinus tropicus* (Krauss, 1848) (Brackenbury and Appleton 1993). In New Zealand, *P. acuta* appears to have replaced the native "*Physastra variabilis*" (syn. *Glyptophysa variabilis*) (Gray, 1843) and may have contributed to a decline in this species by obstructing its feeding or causing physical injury (Winterbourn 1980). The ascendancy of *P. acuta* in Australian rivers typically follows a general decline in the native species present (Zukowski and Walker 2009).

In Argentina, *Physa acuta* has dispersed rapidly, as the species has been recorded only since the 1970s (Paraense 2005). Before that time, this species had been neither cited in the literature nor collected in the field; nevertheless, *P. acuta* has recently become not only widely distributed but also highly abundant in colonized areas (Núñez 2009). Moreover, this species has increased in environments previously inhabited

by the native snail *Stenophysa marmorata* Guilding, 1828, particularly within the Río de la Plata basin. The latter species inhabited mainly lentic, shallow, vegetated areas. *Physa acuta* likewise prefers lentic limno-biotopes, though capable of colonizing a diversity of environments, including anthropogenically altered or polluted habitats. In addition, the high densities in natural populations of *P. acuta* throughout the year contrast sharply with the temporally patchy populations of *S. marmorata* (Núñez 2009).

The omnipresence of *Physa acuta* raises the question of whether this can be the result, in part, from differences in reproductive strategies or in survival compared to *Stenophysa marmorata*. Estimation of demographic rates not only is of interest to life-history theory and population ecology but also is critical for the successful conservation of native species as well as the management of exotics (Frick *et al.* 2010). The purpose of this study was therefore to examine differences in fecundity and survival between these two gastropod species under controlled laboratory conditions.

MATERIALS AND METHODS

Adult *Physa acuta* were collected from an artificial pond (at Saavedra Park) in the city of La Plata (34°55'S, 57°56'W) and *Stenophysa marmorata* from Atalaya beach, in the alluvial-plain area of the Río de la Plata (35°02'S, 57°32'W).

In the laboratory, ovipositions during the first month after collection were used to construct a life table. Individuals born on the same day were separated into 40-ml aquaria (4 individuals maximum per aquarium). The snails were kept in running water without chlorine, at 24 °C under a controlled photoperiod (12 h light, 12 h dark), and fed *ad libitum* with lettuce leaves.

To analyze the life cycle of the two species, I used the horizontal-life-table method (Rabinovich 1972, Begon *et al.* 1988, Rumi 1993), considering zero to be the day when the snails were born. The number of survivors and eggs were grouped into age classes at 7-day intervals. The following values were calculated for each age: N_x = the number of snails expressed as per thousand of the initial value N_0 , l_x = survival, d_x = mortality, q_x = mortality rate, k_x = force of mortality, m_x = fecundity (all specimens were considered female because they are hermaphroditic), e_x = life expectancy, V_x = reproductive value, and R_0 = net reproductive rate.

Ovipositions were monitored daily and the number of eggs per oviposition, the total development time (from laying until hatching), the proportion of hatched eggs, the number of empty eggs, the number of embryos with malformations, and the degree of development reached by the embryos in the eggs that did not hatch were recorded. Embryos in the non-hatched eggs were classified as follows: complete with normal development, partially developed, and undeveloped from the time of laying.

In order to compare the number of eggs per oviposition, and the number of eggs and ovipositions per individual between the species, I used the one-tailed Mann-Whitney test (Zar 1996). This analysis is a nonparametric alternative to the Student's *t*-test, and the samples may be of different sizes. Accordingly, a contingency table tested whether the total number of eggs laid for N_0 (e.g., the replacement rate, R_0) was the same in both species. The proportion of the hatched eggs in each of the two species was also compared through the use of the contingency tables.

The values of e_x were compared by means of the Chi-square test. Correlations between the age of the individuals and the number and size of ovipositions, the average total number of eggs, or the number of hatched eggs per individual were assessed by non-parametric Spearman's coefficients of rank correlation. Correlations between the values of m_x and those of q_x and k_x were also investigated. The program xlstat-Pro 7.5 was used for the statistical analyses.

RESULTS

Stenophysa marmorata ($N_0 = 202$) had a survival curve that was slightly concave (type III, Begon *et al.* 1988), and the highest mortality (d_x) occurred at week 15, when the

population had decreased by more than 50% (Table 1). This species survived for only 60 weeks. Although the highest d_x was registered during the first 20 weeks, the mortality rate (q_x) increased after week 40 (Table 1). The force of mortality (k_x) during the pre-reproductive period was smaller (0.43) than that observed during the two reproductive peaks (1.27 and 0.6).

Physa acuta ($N_0 = 208$) also exhibited a concave survival curve (type III) (Table 2), but even more pronounced than for *Stenophysa marmorata*, because the highest d_x levels were recorded in the first week, with high values maintained until week 16 (Table 2). This species survived for 88 weeks. The mortality rate was quite high during the initial weeks, though a greater increment occurred between weeks 37 and 42 and later between weeks 72 and 80 (Table 2). The force of mortality during the pre- and post-reproductive periods was equal (0.3), but the value was lower than during the reproductive period (1.7). Although at most ages l_x values in *S. marmorata* were higher than in *P. acuta*, the latter species nevertheless had a greater longevity.

Both species laid eggs at night. *Stenophysa marmorata* began to oviposit during week 26 (at about six months), when l_x was 0.37, with a fecundity (m_x) of 0.09 (Table 1). Two reproductive efforts occurred, separated by two weeks. The first, during weeks 26 and 43, had a mean m_x value of 2.5 (*SD*: 1.8), but peaked at 6.7 at week 37. A pause in oviposition occurred, after 3 weeks coinciding with a high q_x . The second reproductive effort occurred over a shorter time period than the first (one month less) and attained a viability of only 0.99% of the original N_0 , but exhibited greater mean m_x (10; *SD*: 7.5) and peaked at 31 during week 50.

Physa acuta began to lay eggs during week 13 with an m_x of 0.25 (Table 2) and an l_x of 0.49. This species reproduced continuously and reached the maximum of m_x (32.5) at week 69. After week 77 these snails had only one more oviposition, with but a single egg, at week 87 whose embryo failed to develop. Therefore, for this species the post-reproductive period extended for 11 weeks.

Although after each reproductive effort mortality rate increased in *Stenophysa marmorata*, this pattern was absent in *Physa acuta*. In *S. marmorata* those data were corroborated by a negative correlation between the values of m_x and q_x and between the values for m_x and k_x , corresponding to Spearman's coefficients of -0.554 ($P = 0.001$) and -0.517 ($P = 0.002$), respectively. These same variables were not significantly correlated in *P. acuta*.

The developmental period was similar for both species (Table 3), but with the mean number of eggs per oviposition being significantly lower in *Stenophysa marmorata* than in *Physa acuta* (Mann-Whitney test, $U = 95021.5$, $Z = -15.6$, $P < 0.0001$). Significant differences were not observed in the number of ovipositions per individual ($P = 0.329$). Moreover,

Table 1. Horizontal life table of *Stenophysa marmorata*. Abbreviations: x , age in weeks; N_x1000 , number of individuals at age x , expressed as a per thousand initial individuals (N_0); d_x , mortality; q_x , mortality rate; k_x , force of mortality; l_x , survival; m_x , fecundity; e_x , life expectancy; V_x , reproductive value at age x on the basis of the total number of eggs; V_{xHE} , reproductive value at age x on the basis of the number of hatched eggs.

x	N_x1000	d_x	q_x	k_x	l_x	m_x	e_x	V_x	V_{xHE}
0	1000	0	0	0	1		22.55	1.09	1.03
1	1000	4.95	0	0	1		21.55	1.17	1.06
2	995.05	0	0	0	1		20.65	1.26	1.10
3	995.05	4.95	0	0	1		19.65	1.35	1.13
4	990.10	39.60	0.04	0.02	0.99		18.75	1.45	1.17
5	950.50	29.70	0.03	0.01	0.95		18.48	1.62	1.25
6	920.79	4.95	0.01	0.00	0.92		18.05	1.79	1.33
7	915.84	4.95	0.01	0.00	0.92		17.14	1.92	1.37
8	910.89	29.70	0.03	0.01	0.91		16.23	2.07	1.42
9	881.19	39.60	0.04	0.02	0.88		15.74	2.29	1.51
10	841.58	34.65	0.04	0.02	0.84		15.44	2.57	1.62
11	806.93	99.01	0.12	0.06	0.81		15.06	2.87	1.74
12	707.92	59.41	0.08	0.04	0.71		16.02	3.51	2.04
13	648.51	4.95	0.01	0.00	0.65		16.40	4.10	2.29
14	643.56	14.85	0.02	0.01	0.64		15.52	4.42	2.37
15	628.71	143.56	0.23	0.11	0.63		14.86	4.85	2.50
16	485.15	4.95	0.01	0	0.49		17.96	6.73	3.33
17	480.20	0	0	0	0.48		17.13	7.28	3.46
18	480.20	24.75	0.05	0.02	0.48		16.13	7.79	3.56
19	455.45	54.46	0.12	0.06	0.46		15.96	8.80	3.86
20	400.99	0	0	0	0.40		16.99	10.70	4.51
21	400.99	0	0	0	0.40		15.99	11.46	4.63
22	400.99	19.80	0.05	0.02	0.40		14.99	12.27	4.77
23	381.19	4.95	0.01	0.01	0.38		14.71	13.83	5.16
24	376.24	4.95	0.01	0.01	0.38		13.89	15.00	5.37
25	371.29	0	0	0	0.37		13.07	16.28	5.60
26	371.29	14.85	0.04	0.02	0.37	0.09	12.07	17.43	5.76
27	356.44	4.95	0.01	0.01	0.36	1.53	11.53	19.34	6.17
28	351.49	24.75	0.07	0.03	0.35	0.75	10.68	19.34	5.80
29	326.73	4.95	0.02	0.01	0.33	1.48	10.41	21.42	5.79
30	321.78	4.95	0.02	0.01	0.32	3.11	9.55	21.68	5.65
31	316.83	14.85	0.05	0.02	0.32	2.94	8.69	20.19	5.16
32	301.98	4.95	0.02	0.01	0.30	1.84	8.07	19.39	4.96
33	297.03	39.60	0.13	0.06	0.30	2.02	7.18	19.11	4.84
34	257.43	9.90	0.04	0.02	0.26	1.46	7.13	21.12	5.45
35	247.52	14.85	0.06	0.03	0.25	2.36	6.38	21.89	5.77
36	232.67	24.75	0.11	0.05	0.23	7.06	5.72	22.25	6.16
37	207.92	4.95	0.02	0.01	0.21	5.14	5.29	18.20	5.86
38	202.97	14.85	0.07	0.03	0.20	2.51	4.39	14.32	5.25
39	188.12	4.95	0.03	0.01	0.19	3.13	3.66	13.65	5.01
40	183.17	103.96	0.57	0.36	0.18	5.86	2.73	11.56	4.49
41	79.21	29.70	0.38	0.20	0.08	4.25	4.00	14.11	6.82
42	49.50	29.70	0.60	0.40	0.05	1.10	4.80	16.90	11.22
43	19.80	0	0	0	0.02	4.00	9.50	42.30	28.85
44	19.80	0	0	0	0.02	0	8.50	41.01	29.67
45	19.80	9.90	0.50	0.30	0.02	0	7.50	43.92	30.51
46	9.90	0	0	0	0.01	4.50	13.00	94.06	62.76
47	9.90	0	0	0	0.01	9.00	12.00	95.90	64.54
48	9.90	0	0	0	0.01	11.00	11.00	93.06	66.38
49	9.90	0	0	0	0.01	5.50	10.00	87.87	64.66
50	9.90	0	0	0	0.01	31.00	9.00	88.21	61.87

Table 1. (Continued)

x	N_x1000	d_x	q_x	k_x	l_x	m_x	e_x	V_x	V_xHE
51	9.90	0	0	0	0.01	20.00	8.00	61.26	45.63
52	9.90	0	0	0	0.01	10.00	7.00	44.18	36.64
53	9.90	0	0	0	0.01	8.50	6.00	36.60	30.49
54	9.90	0	0	0	0.01	10.00	5.00	30.09	25.18
55	9.90	0	0	0	0.01	5.50	4.00	21.52	19.21
56	9.90	4.95	0.50	0.30	0.01	5.50	3.00	17.15	14.62
57	4.95	0	0	0	0	13.00	4.00	24.95	19.78
58	4.95	0	0	0	0	10.00	3.00	12.80	8.00
59	4.95	0	0	0	0	3.00	2.00	3.00	0
60	4.95	4.95	1	0	0	0	1.00	0	0

Table 2. Horizontal life table of *Physa acuta*. Abbreviations: x , age in weeks; N_x1000 , number of individuals at age x , expressed as a per thousand initial individuals (N_0); d_x , mortality; q_x , mortality rate; k_x , force of mortality; l_x , survival; m_x , fecundity; e_x , life expectancy; V_x , reproductive value at age x on the basis of the total number of eggs; V_xHE , reproductive value at age x on the basis of the number of hatched eggs.

x	N_x1000	d_x	q_x	k_x	l_x	m_x	e_x	V_x	V_xHE
0	1000	0	0	0	1		18.93	2.01	1.40
1	1000	129.81	0.13	0.06	1		17.93	2.21	1.50
2	870.19	43.27	0.05	0.02	0.87		19.45	2.79	1.86
3	826.92	76.92	0.09	0.04	0.83		19.42	3.23	2.11
4	750.00	52.88	0.07	0.03	0.75		20.31	3.91	2.50
5	697.11	14.42	0.02	0.01	0.70		20.77	4.62	2.89
6	682.69	24.04	0.03	0.02	0.68		20.19	5.18	3.18
7	658.65	38.46	0.06	0.03	0.66		19.89	5.90	3.55
8	620.19	0	0	0	0.62		20.06	6.88	4.06
9	620.19	14.42	0.02	0.01	0.62		19.06	7.56	4.37
10	605.77	19.23	0.03	0.01	0.61		18.49	8.50	4.81
11	586.54	67.31	0.11	0.05	0.59		18.07	9.64	5.35
12	519.23	24.04	0.05	0.02	0.52		19.28	12	6.50
13	495.19	72.11	0.15	0.07	0.49	0.25	19.16	13.8	7.34
14	423.08	19.23	0.04	0.02	0.42	0.32	21.26	17.4	9.25
15	403.85	38.46	0.09	0.04	0.40	0.21	21.23	19.6	10.42
16	365.39	33.65	0.09	0.04	0.37	0.71	22.36	23.58	12.32
17	331.73	0	0	0	0.33	1.00	23.52	27.67	14.50
18	331.73	0	0	0	0.33	0.23	22.52	29.30	15.39
19	331.73	0	0	0	0.33	0.90	21.52	31.93	16.47
20	331.73	9.62	0.03	0.01	0.33	2.13	20.52	34.08	17.35
21	322.12	4.81	0.02	0.01	0.32	2.31	20.10	36.14	18.50
22	317.31	4.81	0.02	0.01	0.32	3.14	19.39	37.72	19.22
23	312.50	0	0	0	0.31	2.46	18.68	38.58	19.33
24	312.50	4.81	0.02	0.01	0.31	3.86	17.68	39.67	19.85
25	307.69	9.62	0.03	0.01	0.31	3.69	16.94	39.95	19.50
26	298.08	4.81	0.02	0.01	0.30	4.53	16.45	41.11	19.81
27	293.27	0	0	0	0.29	4.89	15.71	40.84	20.15
28	293.27	4.81	0.02	0.01	0.29	3.98	14.71	39.49	20.17
29	288.46	24.04	0.08	0.04	0.29	4.20	13.93	39.65	20.46
30	264.42	4.81	0.02	0.01	0.26	4.04	14.11	42.48	22.21
31	259.62	0	0	0	0.26	8.59	13.35	43.01	22.61
32	259.62	0	0	0	0.26	7.13	12.35	37.81	15.09
33	259.62	9.62	0.04	0.02	0.26	6.59	11.35	33.70	13.67
34	250.00	24.04	0.10	0.04	0.25	7.96	10.75	30.92	12.76
35	225.96	24.04	0.11	0.05	0.23	6.19	10.79	27.90	11.83

Table 2. (Continued)

x	$N_x/1000$	d_x	q_x	k_x	l_x	m_x	e_x	V_x	$V_x H E$
36	201.92	24.04	0.12	0.06	0.20	3.71	10.95	26.68	12.09
37	177.89	48.08	0.27	0.14	0.18	4.22	11.30	28.63	13.21
38	129.81	19.23	0.15	0.07	0.13	3.26	14.11	36.75	18.12
39	110.58	28.85	0.26	0.13	0.11	3.09	15.39	43.19	21.22
40	81.73	9.62	0.12	0.05	0.08	3.29	19.47	59.59	28.56
41	72.12	0	0	0	0.07	2.60	20.93	70.08	34.12
42	72.12	14.42	0.20	0.10	0.07	9.13	19.93	74.12	34.43
43	57.69	0	0	0	0.06	7.83	23.67	89.23	39.96
44	57.69	4.81	0.08	0.04	0.06	10.17	22.67	89.41	39.87
45	52.89	0	0	0	0.05	13.09	23.64	94.96	37.52
46	52.89	4.81	0.09	0.04	0.05	9.09	22.64	89.92	32.46
47	48.08	0	0	0	0.05	12.50	23.80	97.67	35.10
48	48.08	0	0	0	0.05	16.90	22.80	93.55	32.08
49	48.08	0	0	0	0.05	7.40	21.80	84.19	27.96
50	48.08	0	0	0	0.05	17.80	20.80	84.35	27.41
51	48.08	0	0	0	0.05	5.10	19.80	73.10	22.61
52	48.08	4.81	0.10	0.05	0.05	2.60	18.80	74.70	21.11
53	43.27	0	0	0	0.04	9.67	19.78	87.99	25.01
54	43.27	0	0	0	0.04	7.67	18.78	86.03	26.56
55	43.27	0	0	0	0.04	5.89	17.78	86.08	28.23
56	43.27	0	0	0	0.04	3.78	16.78	88.08	29.19
57	43.27	0	0	0	0.04	13.56	15.78	92.60	29.86
58	43.27	0	0	0	0.04	15.33	14.78	86.83	30.47
59	43.27	0	0	0	0.04	24.33	13.78	78.53	22.63
60	43.27	0	0	0	0.04	10.00	12.78	59.53	12.88
61	43.27	4.81	0.11	0.05	0.04	2.89	11.78	54.40	10.52
62	38.46	4.81	0.13	0.06	0.04	1.50	12.13	63.66	12.60
63	33.65	4.81	0.14	0.07	0.03	8.86	12.71	78.03	15.50
64	28.85	0	0	0	0.03	16.33	13.67	88.64	19.29
65	28.85	0	0	0	0.03	4.33	12.67	79.43	17.53
66	28.85	0	0	0	0.03	8.50	11.67	82.48	17.62
67	28.85	0	0	0	0.03	7.83	10.67	81.26	18.96
68	28.85	0	0	0	0.03	11.33	9.67	80.66	20.05
69	28.85	0	0	0	0.03	0	8.67	76.15	15.13
70	28.85	0	0	0	0.03	32.50	7.67	83.64	16.28
71	28.85	4.81	0.17	0.08	0.03	23.17	6.67	56.18	8.73
72	24.04	9.62	0.40	0.22	0.02	22.20	6.80	43.51	5.47
73	14.42	0	0	0	0.01	22.67	9.67	39.01	4.07
74	14.42	0	0	0	0.01	0.67	8.67	17.95	1.87
75	14.42	0	0	0	0.01	7.00	7.67	18.99	2.01
76	14.42	0	0	0	0.01	0	6.67	13.17	2.17
77	14.42	4.81	0.33	0.18	0.01	14.33	5.67	14.46	2.33
78	9.62	0	0	0	0.01	0	7.00	0.22	0
79	9.62	0	0	0	0.01	0	6.00	0.24	0
80	9.62	4.81	0.50	0.30	0.01	0	5.00	0.26	0
81	4.81	0	0	0	0.01	0	8.00	0.57	0
82	4.81	0	0	0	0.01	0	7.00	0.63	0
83	4.81	0	0	0	0.01	0	6.00	0.69	0
84	4.81	0	0	0	0.01	0	5.00	0.76	0
85	4.81	0	0	0	0.01	0	4.00	0.83	0
86	4.81	0	0	0	0.01	0	3.00	0.91	0
87	4.81	0	0	0	0.01	1.00	2.00	1.00	0
88	4.81	4.81	1.00	0	0.01	0	1.00	0	0

Table 3. Characterization of the ovipositions by *Stenophysa marmorata* and *Physa acuta*.

Attributes	<i>S. marmorata</i>	<i>P. acuta</i>
Total number of ovipositions	466	855
Total number of eggs	2,434	8,203
Mean (SD) number of eggs per oviposition	5.17 (2.37)	9.58 (6.35)
Maximum number of eggs per oviposition	17	50
Minimum number of eggs per oviposition	1	1
Mean (SD) time of embryonic development (days)	17 (7.32)	14 (7)

the proportion of hatched eggs was greater in *P. acuta* than in *S. marmorata* (Contingency table, Chi-square = 135.2, $P < 0.0001$). In the latter species, fewer than one-third of the eggs hatched, and more than one-half of the embryos were not developed (Fig. 1). In addition, 103 empty eggs were recorded; two being with two embryos, with one of those embryos having a lethal cephalic malformation and the other hatching without a shell. In *P. acuta*, two eggs without an embryo and another two with two embryos were observed. Nearly half of the eggs hatched, whereas one-third failed to continue development (Fig. 1). Two embryos exhibited cephalic malformations and did not hatch, while another was born without a shell.

Physa acuta had significantly higher values of m_x compared to *Stenophysa marmorata*, on the basis of either the total

number of eggs per individual (Mann-Whitney test, $U = 926.5$, $Z = -1.5$, $P = 0.063$) or hatched eggs per individual (Mann-Whitney test, $U = 953$, $Z = -1.3$, $P = 0.091$). In addition, *P. acuta* had a more-lengthy reproductive period. The total number of eggs laid by individuals during the entire reproductive period, calculated as the sum of the m_x values, was only about 200 in *S. marmorata*, but over 480 in *P. acuta*.

In *Physa acuta*, the mean number of eggs per oviposition increased with the snails's age, and a significant correlation existed (Fig. 2). This relationship was not observed in *Stenophysa marmorata* (Fig. 2). In both species, however, the total number of eggs and ovipositions per specimen increased with the gastropods' age, with that correlation being greater in *S. marmorata* (Figs. 3, 4). On the basis of only the hatched eggs per individual, a positive correlation with age was observed in *S. marmorata*, whereas this relationship did not

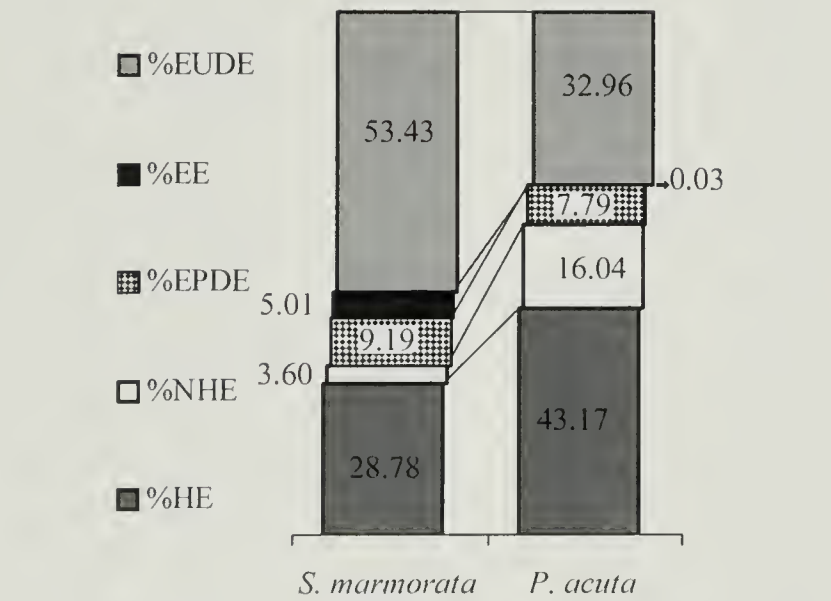


Figure 1. Percentage of hatched eggs (HE), non-hatched eggs with complete and normally developed embryos (NHE), eggs with partially developed embryos (EPDE), eggs with undeveloped embryos (EUE), and empty eggs (EE) among the total eggs laid by *Stenophysa marmorata* and *Physa acuta*.

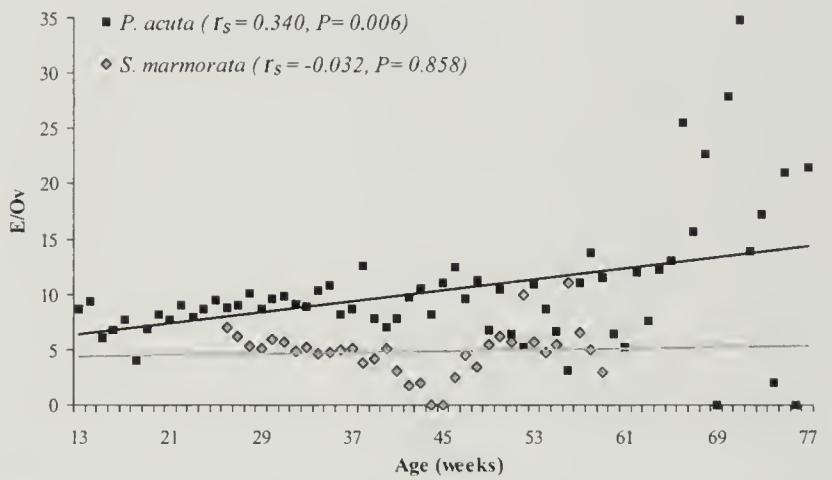


Figure 2. Mean number of eggs per oviposition (E/Ov) per age in *S. marmorata* ($N = 34$) and in *P. acuta* ($N = 65$). r_s , Spearman's Correlation Coefficient.

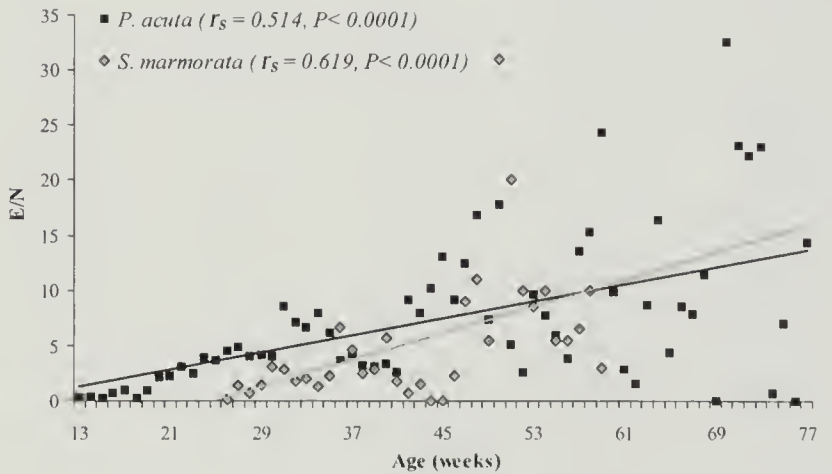


Figure 3. Mean number of eggs laid per individual (E/N) at each age in *S. marmorata* ($N = 34$) and in *P. acuta* ($N = 65$). r_s , Spearman's Correlation Coefficient.

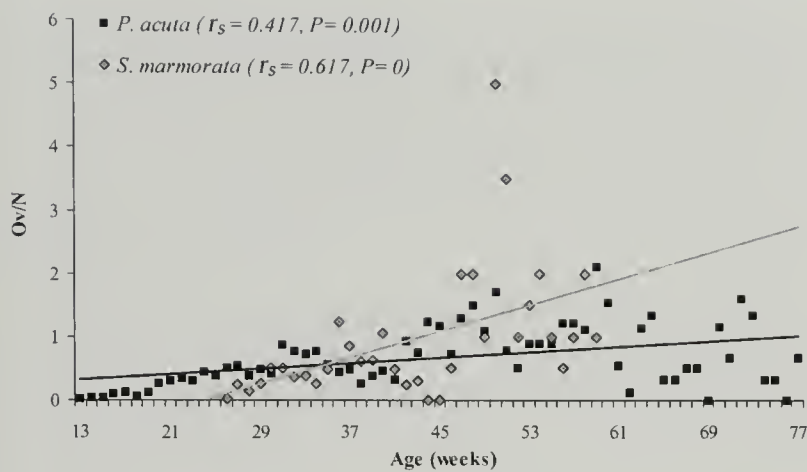


Figure 4. Mean number of ovipositions per individual (Ov/N) at each age in *S. marmorata* ($N = 34$) and in *P. acuta* ($N = 65$). r_s , Spearman's Correlation Coefficient.

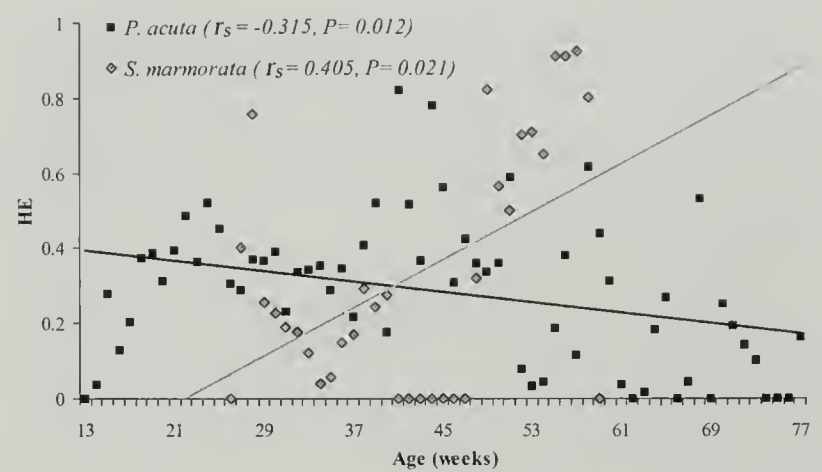


Figure 6. Mean of hatched eggs (HE) at each age in *S. marmorata* ($N = 34$) and in *P. acuta* ($N = 65$). r_s , Spearman's Correlation Coefficient.

occur in *P. acuta* (Fig. 5). This difference resulted because in *S. marmorata* the proportion of hatched eggs tended to increase with age, but in *P. acuta* this parameter showed an age-associated decrease (Fig. 6).

Life expectancy (e_x) exhibited a similar profile with age in both species, but with consistently higher values for *Physa acuta* (Chi-square $\chi^2 = 247.1$, $df = 59$). In both species a decrease occurred from week 22 on, but during approximately the fortieth week a new increase began (Tables 1-2). In *Stenophysa marmorata*, e_x values peaked at 13 in week 46, but was not greater than during the first weeks (with a maximum of 22.6 in week 1). In contrast, *P. acuta* reached its maximum e_x of 23.8 at week 47.

In *Stenophysa marmorata*, V_x increased between weeks 43 and 54, ranging from 30.1 to 95.9 (Table 1). Individuals of those ages, therefore, make a higher contribution to the next generation. In *Physa acuta* high values of V_x occurred for a

more extensive length of time, between weeks 39 and 72, with values between 43.2 and 97.7 (Table 2).

Moreover, the mean number of offspring produced per individual of *Stenophysa marmorata* throughout its entire life was 12.1 (the replacement rate, or R_0), less than one-third of that in *Physa acuta*, 39.4. This difference was highly significant ($P < 0.0001$).

When only hatched eggs were considered, in *Stenophysa marmorata*, the m_x value diminished, while the period without viable eggs (between the two reproductive efforts) extended from 2 to 7 weeks. In addition, the values of V_x decreased (Table 1) and especially those of R_0 , which dropped to 2.93, only one-fourth of its original value. In *Physa acuta* m_x , V_x , and R_0 likewise declined, but less than in *S. marmorata* (Table 2); while the net reproductive rate decreased by nearly one-half (15.0), it still remained fivefold higher than the observed value in *S. marmorata*.

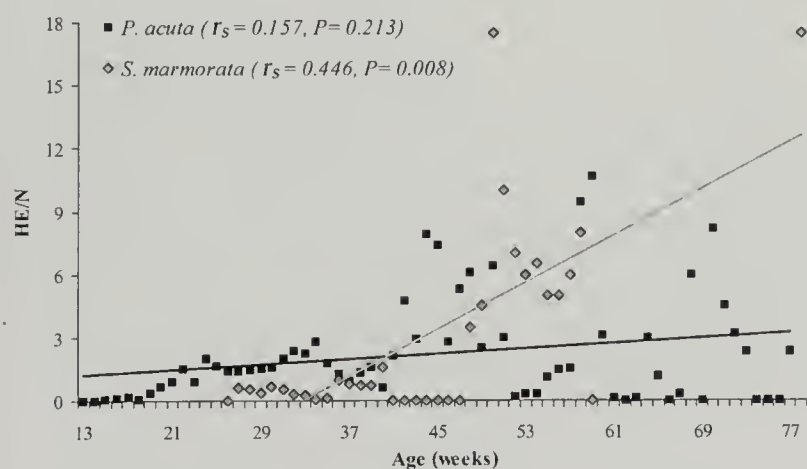


Figure 5. Mean number of hatched eggs per individual (HE/N) at each age in *S. marmorata* ($N = 34$) and in *P. acuta* ($N = 65$). r_s , Spearman's Correlation Coefficient.

DISCUSSION

Results obtained in the laboratory indicate a more successful reproductive strategy in the exotic snail, as compared to the native, corroborating field observations, where *Stenophysa marmorata* exhibits a markedly seasonal reproductive cycle. *Physa acuta*, in contrast, reproduces during the entire year and at these latitudes is not limited temperatures cold enough to freeze the water, as in the Northern Hemisphere, and begins to reproduce at a smaller size (Núñez 2009).

The pre-reproductive period of *Physa acuta* was only half as long as that of *Stenophysa marmorata*. Although the length of this interval depends on the temperature (Thomas and McClintock 1990), in this circumstance temperature conditions

were the same for both species. In contrast to Clampitt (1970), the more extended reproductive period and lower individual growth rate of *P. acuta*, as compared to *S. marmorata* (Núñez 2009), does not indicate that the former requires more stable environments; on the contrary, *P. acuta* is found in a wider variety of environments.

Both *Physa acuta* and *Stenophysa marmorata* are able to inhabit semi-permanent habitats although neither can survive in the absence of water (Núñez 2009). Nevertheless, the earlier sexual maturation of *P. acuta* enables it to either repopulate or colonize other environments more easily than *S. marmorata*. Moreover, the laboratory results here, with respect to greater fecundity values and higher percentages of viable eggs, apart from that more rapid maturation, corroborate the existence of reproductive characteristics giving a distinct colonization and survival advantage over the latter species.

In the field, I observed competition for space that has resulted in reduction in both the density and the area of occupation of *Stenophysa marmorata* although up until the present no competitive exclusion has occurred (Núñez 2009). The same form of exclusion could presumably occur with *Biomphalaria peregrina* (d'Orbigny, 1835) (Planorbidae). In artificial lakes of recent origin in the north of the Buenos Aires Province, *Physa acuta* was among the first species colonizing those environments, together with the native *Pomacea canaliculata* (Lamarck, 1822) (Ampullariidae), *Heleobia parchappii* (d'Orbigny, 1835) (Cochliopidae), and more belatedly, *B. peregrina* (Núñez 2009). The first of these species was located at greater depths, and the second over substrate in shallow water, whereas *B. peregrina* colonized submerged vegetation, where *P. acuta* was also present. However, *B. peregrina* never attained the same densities as the other three species. Under laboratory conditions, it began reproduction later than *P. acuta* (at week 17), had a shorter reproductive period (30 weeks), and had lower fecundity values (Rumi 1993). The appearance of *P. acuta* in limnobiomes within Argentina thus apparently reduces species richness and diversity through altering relative abundances of the native gastropods.

According to Rankin and Harrison (1979), *Stenophysa marmorata* is an r-selected, pioneering species capable of rapid exploitation of favorable conditions, but this study indicates that those characteristics are more pronounced in *Physa acuta*.

My results are in accord with the characteristics proposed for *Physa acuta* by Dillon and Wethington (2004), e.g., early sexual maturation and high reproductive rates. According to the USR model of life history variation in freshwater molluscs, populations are classified in U-populations, Undifferentiated with respect to reproductive effort, S-adapted, for Stress-tolerant, and R-adapted, for Reproductive recklessness (Dillon 2000). Both of these species could be classified as R-strategists although *Stenophysa marmorata* devotes more energy to growth at the

cost of later maturation and longevity in comparison to *P. acuta*, and the latter is iteroparous. On the basis of all these characteristics, *P. acuta* has reproductive characteristics typical of a highly invasive species (Morton 1996).

Dillon and Wethington (2004) demonstrated that intraspecific variation exists in the life histories of different populations and attributed this variability to the diversity and spatial isolation of the habitats from which those populations arose. Even though in this instance the two snail populations used in these laboratory experiments were separated by less than 7' in latitude and 24' in longitude, the differences were still statistically significant.

Despite the similarity that the two species exhibited in the distribution of the mortality, *Stenophysa marmorata* survived for a much shorter time because reproduction affected survival. Both of these snails suffered high mortality during initial weeks; nevertheless, both the mortality rate and the force proved greater around week 40, and neither survival curve was as markedly concave as the curves previously observed for *Biomphalaria peregrina*, likewise under laboratory conditions (Rumi 1993).

Although laboratory experiments necessarily underestimate mortality, the similar conditions allow comparison of populational parameters (i.e., life expectancy, reproductive value, and net reproductive rate) which indicate populational-growth potential is demonstrably greater in the exotic species.

Therefore, the high worldwide distribution as well as the omnipresence of the exotic *Physa acuta* with respect to the native *Stenophysa marmorata* in Argentina could be explained, at least in part, by early sexual maturation, higher reproductive potential, and greater longevity. The importance of interspecific competition between these two species needs, however, to be the subject of further study.

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